Ecologists Gather for Mix of Policy, Science in Nashville

Nearly 4000 ecologists and plant biologists gathered in Knoxville, Tennessee, from 7 through 11 August for the joint meeting of the American Institute of Biological Sciences, which was dominated by the 7400-member-strong Ecological Society of America (ESA). In keeping with this year's theme of science and public policy, the meeting featured a hefty dose of applied science as well as plenty of basic research.

Model Predicts "Extinction Debt"

One talk that bridged the gap between abstruse mathematics and environmental issues came from theoretical ecologist David Tilman of the University of Minnesota in St. Paul. He offered some alarming conclusions about the pattern of species extinctions that is likely to result from the habitat destruction now under way in many parts of the world.

Tilman described a mathematical model that predicts a time lag between habitat loss and extinction. This is alarming, he said, because it means that species that appear to be faring well may already be doomed to extinction in the next hundred years or so, even if their remaining habitat is preserved. "Given the habitat destruction already done, we've already incurred a massive 'extinction debt,'" Tilman said in his talk. "We as ecologists are grossly underestimating the magnitude of extinction." Equally disturbing, he says, is the finding that the species most likely to vanish are the best competitors in the habitat—an unexpected conclusion likely to send ripples through the ecological community.

Tilman developed his model, which was published in *Ecology* in January, by studying the diversity of plants in grassland communities, specifically the old fields and prairie at Cedar Creek Natural History Area in Minnesota. The model describes each species as a "metapopulation"—a set of small, local populations that live in scattered sites but are linked by their ability to disperse seeds and sprout in more distant places.

Such metapopulation models are all the rage, but Tilman's adds a new twist based on his observations at Cedar Creek. He found that the best competitors for resources are also the poorest at dispersal. For example, bluestem grasses have extensive roots and outcompete their neighbors in absorbing nitrogen from the soil. But because these grasses pump so much energy into their roots, they produce relatively few seeds. By building the concept of a trade-off between competitive ability and dispersal into his model, Tilman predicted the coexistence of the many plant types at Cedar Creek.

In the work presented at ESA (and in press at *Nature*), Tilman, with Minnesota's Clarence Lehman and Robert May and Martin Nowak of Oxford University in England, went on to calculate the effects of habitat loss on extinctions. They found that diversity losses were relatively modest even after a large proportion of habitat—50% or more—was destroyed. But at a certain level, incremental habitat losses led to a dramatic rise in the extinction rate. "The 'good news' is that if you destroyed half the Earth, you'd lose only about 10% of the species," Tilman said. "But the bad news is...as you near 60%–70%–80% habitat loss, a very slight increase in destruction leads to a sharp increase in the number of species lost."

Furthermore, thanks to the dynamics of metapopulations, there was a time lag of several generations or more between habitat loss and extinction. Part of the reason is that destroying a habitat not only wipes out existing populations, it also removes potential colonization sites. When older subpopulations eventually succumb to local threats, the entire metapopulation will die out. Top competitors proved particularly susceptible to this effect, as they're not very good at dispersing anyway.

For ecologist Gordon Orians of the University of Washington, this was the real surprise in Tilman's work—that top competitors were the most vulnerable. Tilman himself called this "a disturbing prediction of the theory. As extinctions occur, ecosystems disproportionately lose the species best adapted to use the resources in those habitats." That's worrisome because top competitors are valuable members of ecosystems, often playing a key role in keeping ecosystems productive and sustainable. For example, bluestem grasses are important in retaining nitrogen in the Cedar Creek ecosystem.

Orians notes, however, that more work will be needed to test the key assumption on which the model is based—the trade-off between dispersal and competitive ability. "That's an absolutely critical assumption that may not always be true," he says. Indeed, he predicts that one of the benefits of this research will be a flurry of new work on the relationship between competitive ability and dispersal.

Tilman agrees that more testing needs to be done to see if the trade-off holds in other communities. In fact, given the grim ecological consequences, he told meeting attendees that in this case he's actually hoping his model will turn out to be wrong.

The Weeds That Swallowed the West

In the vast rangelands of the American West, many ecosystems face a new public enemy number one: alien plants that are sweeping across the landscape at exponential rates. Once considered just an agricultural problem, these invaders are proving to be the single greatest threat to natural ecosystems in the West, said Jerry Asher, research coordinator at the Bureau of Land Management (BLM) in Portland, Oregon, in his talk at the meeting.

These Eurasian immigrants compete with native plants, increase soil erosion, and can transform wetlands, prairies and hillsides into stands of alien species. Ben Roche, a specialist in exotic plant ecology at Washington State University in Pullman, thinks something has to be done: "If we want to go on maintaining the kinds of plant communities that are native on federal lands, then things have got to change."

To reach these conclusions, BLM officials surveyed plant populations on the 180 million acres of land they manage, and Asher talked to a host of scientists and land managers dealing with exotic plants. The data on BLM lands show that alien plants are expanding their territory by 14% each year—which amounts to a whopping 2300


JERRY E. ASHER

"Worst of the worst." The tough Eurasian weed leafy spurge, shown here covering an entire field, is extremely hard to kill.

acres taken over by the plants every day.

And although land that has been previously disturbed is at highest risk for invasion, even parks and wilderness areas are at risk. For example, Grand Teton National Park now hosts unwanted invaders such as spotted knapweed (from central Europe), musk thistle (known from Eurasia), and dalmation toadflax (from near the Adriatic Sea). More than 60% of the 1350 acres that make up Devil's Tower National Monument in Wyoming have been infested by exotic plants, mostly leafy spurge (*Euphorbia esula*), an alien Asher calls "the worst of the worst." Once established, this plant is almost impossible to kill because its roots plunge 20 feet into the ground. "You can plow, you can spray, you can do whatever you want. It just comes back," says Asher.

Leafy spurge, like many of the other exotics, arrived in the United States sometime in the 1800s and became established in the West around the turn of the century, says Roche. Many such plants were imported by settlers eager for a touch of home; others were accidentally transported in ships' holds. Already adapted to a relatively dry climate and freed from their native predators and parasites, the plant populations followed the classic exponential growth curve, steadily doubling their numbers as well as moving into new regions. Today, many species have reached a stage where their numbers are large enough to be a major problem—and their populations are still growing. The net effect is what Asher calls an explosion in slow-motion.

Take "rush skeletonweed" (*Chondrilla juncea*), which is originally from the Balkans and is named for the leggy twigs it sports in place of leaves. Two plants were spotted on the outskirts of Banks, Idaho, in 1954. Ten years later, skeletonweed had invaded 40 acres; today, land managers battle the plant on 4 million acres in Idaho alone, says Asher. Not all of that land is a monoculture of skeletonweed, but some areas are. And once covered by a sea of exotic weeds, "for all practical purposes, that land is gone," says Asher. Diversity drops, erosion rises, and ecosystems become a patchwork of undesirable species.

For example, in the Sellway/Bitterroot Wilderness in Idaho, which includes prime stream habitat for endangered salmon, some riverbanks are blanketed with Eurasian spotted knapweed (*Centaurea maculosa*). Between the plants is bare soil, and when it rains, that soil washes into the river. The extra silt settles into the gravel of the riverbed, degrading the salmon spawning grounds.

The West isn't the only region waging war against exotic plants. Other presentations and posters at the meeting detailed the ravages of invaders such as *Polygonum perfoliatum*, or mile-a-minute weed, which is spreading southward along Mid-Atlantic roadsides. In Haleakala National Park on the island of Maui, Hawaii, land managers are attempting to protect the park's many endangered species against waves of alien plants and animals. Their newest experimental tactic: Shooting harpoons full of herbicide into the trunks of *Miconia calvescens*, an invasive neotropical tree.

But biologists who want to heed Roche's plea that "things have got to change" have their work cut out for them. In the West, Asher and others are trying to encourage managers to nab aliens early, when stands are small enough to be sprayed or pulled by hand. For large areas already covered by weeds, the preferred option is to even the balance by importing the aliens' natural predators from their homeland. But so far, says Asher, the weeds are winning.

Growing Into the Gap

For a young tree struggling to survive in the dark understory of a tropical rainforest, the toppling of a mature tree nearby is truly a windfall. When a big neighbor comes crashing down, a gap opens in the forest canopy, allowing light to penetrate to the shadowy floor. For years, the conventional wisdom has held that gaps do more than benefit individual trees: They were also thought to nurture the growth of a rich mix of species with varying light preferences, thus maintaining the diversity of the entire forest.

But provocative new data presented at the meeting by ecologist Stephen Hubbell of Princeton University dealt a blow to this seemingly logical reasoning. Contrary to the predictions of this hypothesis, Hubbell found little difference in the diversity of saplings between gap and nongap sites in an 8-year study on Barro Colorado Island in Panama. Gaps may still play some role in fostering diversity, Hubbell concludes, but the processes involved don't follow the traditional model.

According to that view, because gaps create a gradient of light—from about 1% to 20% of full sunlight—they encourage growth of a variety of species with different light preferences. Hubbell and his colleagues Robin Foster of the Field Museum of Natural History in Chicago and Richard Condit of the Smithsonian Tropical Research Institute reasoned that if this were true, areas with recent gaps ought to accumulate species relatively rapidly. In contrast, areas with no recent gaps should show a gradual decline in diversity, as the effects of ancient gaps waned.

To test this notion, from 1982 through 1990 Hubbell and his colleagues tracked sapling abundance and diversity in more than 600 gaps and nongap sites in a 50-hectare plot of high-canopied forest on Barro Colorado. The results were surprising, Hubbell says. Saplings were more numerous in gaps than in nongap sites. But the relative abundances of most species were similar in gaps and nongaps and did not change during the 8 years. Rather than favoring one set of trees over another, it seems gaps simply allow the existence of more young trees per unit area, Hubbell says.

Even in the face of these results, Hubbell isn't concluding that gaps have no effect on diversity. He favors a model in which gaps promote diversity indirectly. In this view, the true diversifying force is not the gap itself but the dispersal limitations that determine which species are present when the gap opens. "The influence of the gap is essentially over after the first few months of gap creation," he said.

After the talk, Hubbell was surrounded by a crowd eager for more details of the work; he promised to finish his paper soon. Once published, the research is likely to spark quite a bit of controversy, and perhaps signal a shift in emphasis in gap studies, predicts Peter Ashton of Harvard University, who was not at the talk but is familiar with the research. Ashton, who has collaborated with Hubbell in the past, considers the work a "useful corrective" for the field.

STEVE HUBBELL

Forest gap. Gaps in the forest canopy may be less important than thought for fostering species diversity.

Indeed, even some who once championed the traditional view say this and other new research are slowly shifting the prevailing view of how gaps promote diversity. Variations in trees' response to light still may play a role, says forest ecologist Julie Denslow of Tulane University, "but it may not explain the coexistence [of many species] as neatly as we thought it did." And that implies that a new gap may be opening in ecologists' knowledge of how tropical forests achieve their great diversity.

–Elizabeth Culotta